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Native Fauna on Exotic Trees: Phylogenetic Conservatism and Geographic Contingency in Two Lineages of Phytophages on Two Lineages of Trees

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ABSTRACT: The relative roles of evolutionary history and geographical and ecological contingency for community assembly remain unknown. Plant species, for instance, share more phytophages with closer relatives (phylogenetic conservatism), but for exotic plants introduced to another continent, this may be overlaid by geographically contingent evolution or immigration from locally abundant plant species (mass effects). We assessed within local forests to what extent exotic trees (Douglas-fir, red oak) recruit phytophages (Coleoptera, Heteroptera) from more closely or more distantly related native plants. We found that exotics shared more phytophages with natives from the same major plant lineage (angiosperms vs. gymnosperms) than with natives from the other lineage. This was particularly true for Heteroptera, and it emphasizes the role of host specialization in phylogenetic conservatism of host use. However, for Coleoptera on Douglas-fir, mass effects were important: immigration from beech increased with increasing beech abundance. Within a plant phylum, phylogenetic proximity of exotics and natives increased phytophage similarity, primarily in younger Coleoptera clades on angiosperms, emphasizing a role of past codiversification of hosts and phytophages. Overall, phylogenetic conservatism can shape the assembly of local phytophage communities on exotic trees. Whether it outweighs geographic contingency and mass effects depends on the interplay of phylogenetic scale, local abundance of native tree species, and the biology and evolutionary history of the phytophage taxon.

Keywords: alien species, coevolution, community assembly, insect herbivores, taxonomic isolation, mass effect.

Introduction

Which factors shape the assembly of local species communities? The influences of natural selection, phylogenetic history, and ecological context (e.g., variation in the abundance of particular species) and how these factors interact have been identified as key issues to be addressed in community ecology (Agrawal et al. 2007). Entomologists have long stressed the role of evolutionary history in the assembly of communities of phytophagous insects, which represent a major part of Earth's biodiversity (Ehrlich and Raven 1964; Ives and Godfray 2006; Murakami et al. 2007). Coevolutionary processes have been shown to play a major role in explaining today's differences in phytophagous communities between plant species. Moreover, in particular for trees, it has been demonstrated that related species share similar chemical and physical traits and therefore share similar phytophage communities (Futuyma and Gould 1979; Neuvonen and Niemelä 1983; Frenzel and Brandl 2001; Novotný et al. 2002a, 2002b; Brändle and Brandl 2006). Both coevolution between insects and plants and the conservation of functional plant traits result in phylogenetic conservatism of phytophage communities on plants: plant species within the same lineage share more phytophages than do species from different lineages. In such a scenario of phylogenetic conservatism, both plants and phytophages live in a highly predictable world, exerting the same mutual selection pressure across their entire range, which increases the probability of mutual specialization, resulting in stabilizing selection and thus further phylogenetic conservatism (or in mutual arms races; Vermeij 1993; Ackerly 2003). The dynamics of populations are essentially driven by the evolutionary history

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of species, and less so by their idiosyncratic interactions with local environments (Price 2003).

Plant lineages, however, may evolve differently in different parts of the world; this can be referred to as geographic contingency. Classical examples of contingent evolution of traits are convergent evolution of the same traits by different lineages occurring in different parts of the world (Walter and Breckle 1991), founder effects in the evolution of lineages on islands (Silvertown 2004), or geographic mosaics of coevolution (Thompson 1999). Also, the same plant lineages can evolve in different abiotic and biotic niches in different parts of the world, resulting in different coevolutionary processes (Armbruster and Baldwin 1998; Pärtel 2002). Such geographic contingencies may have major impacts on community assembly (Thompson 1999). In particular, it is not clear whether a plant species that moves from one continent to another would be expected to be colonized by phytophages from the most closely related native plant species (from which the immigrant has been separated for millions of years). In other words it is not clear whether phylogenetic conservatism still drives the assembly of phytophage communities in this situation or whether it has been overridden by geographic contingency.

Phylogenetic conservatism in the assembly of arthropod communities on exotic plant species might also be overridden by local mass effects, that is, the influx of individuals from large source populations in surrounding habitats or host patches (Shmida and Wilson 1985). It can be supposed that the ecological rather than the phylogenetic opportunity might be a major determinant in colonization of exotic plants (Strong et al. 1984). The more abundant a plant is in a particular system, the more abundant are its associated arthropod communities. Hence, colonization of an exotic plant might be merely an effect of a higher probability that the plant is reached by more abundant insect species. This is exemplified by the study of Winter (1974), in which the major colonization of introduced conifers originated from abundant but unrelated native moorland plants.

Trees represent one system for studying the role of phylogenetic conservatism in the colonization of exotic plant species by phytophages. Sources of arthropod colonists of trees can be meaningfully split into four broad types: (1) the most closely related tree species available, (2) intermediately distantly related tree species that are still from the same phylum, (3) very distantly related tree species that are from a different phylum (usually gymnosperms or angiosperms), and finally, (4) the herb and shrub layer in which the trees were planted. In temperate forests, the herb and shrub layer is usually at least intermediately distantly related to exotic tree species, that is, it belongs to a different family or even phylum (with some exceptions,

such as honey locust and understory legumes). But for a young exotic tree, the herb and shrub layer spatially harbors by far the most proximate pool of arthropods, offering a strong ecological opportunity for colonizers (mass effects; Winter 1974). These colonizations might be conserved to some degree when trees get older (despite ongoing species turnover; e.g., Crawley 1983; Warner and Cushman 2002).

Our current understanding of the role of phylogenetic proximity for the colonization of exotics from natives is highly contradictory. The few studies performed revealed significant similarities between communities on exotic species and closely related natives, but these studies either focused on species richness and not faunal composition (Lawton and Schröder 1977; Conner et al. 1980; Neuvonen and Niemelä 1981; Kennedy and Southwood 1984; Brändle and Brandl 2001) or effect sizes were quite low (Roques et al. 2006). Winter (1974) even showed that, at least in some cases, colonization from the distantly related surrounding herb and shrub layer may be important. Moreover, Frenzel et al. (2000) found no correlation between phylogenetic proximity and species richness for exotic tree genera in Germany. The reason for the inconclusiveness of the results may be that these studies did not examine local communities, but instead compiled species lists of phytophages across entire regions. Such data compiled from published lists may suffer from unknown inaccuracies (e.g., Fagan and Kareiva 1997; Ponder et al. 2001; Kadmon et al. 2004). Moreover, the species pools of local communities, patterns of coevolution, and host-plant use (Thompson 1999) may vary within regions, obscuring factors driving the assembly of local communities. Although local approaches such as sampling coexisting tree species have disadvantages as well (e.g., the composition of local community samples may strongly depend on the trapping methods used), such local approaches are needed to verify the role of phylogenetic proximity for the local colonization of exotic tree species by native insects and to test for mass effects due to locally abundant source pools. Such analyses are still missing.

In central European forests, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and American red oak (*Quercus rubra* L.) are among the most abundant exotic coniferous and broad-leaved tree species, respectively. Douglas-fir was first introduced from western North America to central Europe in 1827, and red oak was introduced from eastern North America in 1691 (Knoerzer and Reif 2002), with rates of plantation increasing for both at the end of the nineteenth century. In southern Germany, Douglas-fir frequently occurs together with Norway spruce (*Picea abies* L.) and beech (*Fagus sylvatica* L.) and more rarely with silver fir (*Abies alba* Mill.). These are cases of small (Douglas-fir vs. Norway spruce), intermediate (Douglas-fir vs. silver fir), and large

(Douglas-fir vs. beech) phylogenetic distance. Red oak occurs together with pedunculate oak (*Quercus robur* L.), beech, and Norway spruce, representing small (red oak vs. pedunculate oak), intermediate (red oak vs. beech), and large (red oak vs. Norway spruce) phylogenetic distances.

We used Douglas-fir and red oak to test the role of phylogenetic conservatism for the assembly of phytophage communities, that is, whether and to what extent more phytophages are recruited from closely related native tree species than from distantly related sources. We performed analyses using faunal dissimilarity measures emphasizing both the overall phytophage fauna and the fauna of numerically dominant phytophage species, that is, the major drivers of tree/phytophage interactions. Then, to explore to what extent mass effects can blur phylogenetic conservatism in the assembly of phytophages on exotic trees, we analyzed whether faunas on Douglas-fir become increasingly similar to those on the distantly related beech with an increasing abundance of beech in the forest canopy. Moreover, we tested to what extent Douglas-fir or red oak shared more species with the (at least intermediately distantly related) ground vegetation among which the trees grew than with closely related canopy trees. We applied a local approach to studying phytophages on trees coexisting within the same forest, and we considered two taxa of phytophages with different levels of specialization: highly specialized sap-feeding true bugs and less specialized chewing beetles. Among the Coleoptera, we further differentiated between those clades that evolved before and those that evolved during or after the angiosperm radiation.

Material and Methods

Study Site

The study was conducted in three mature forest sites (tree age >100 years) in southern Bavaria, Germany, in the years 1999–2001: Oberschönegger Forst, near Dietershofen (10°21'E, 48°06'N); a private forest near Edelstetten (10°25'E, 48°17'N; both for studying Douglas-fir); and Ettenbeurer Forst, near Ettenbeuren (10°24'E, 48°22'N; for red oak). Altitudes are 620–645 m asl for Dietershofen, 550 m asl for Edelstetten, and 530 m asl for Ettenbeuren. Mean annual precipitation is higher at Dietershofen (850–900 mm) than at Edelstetten and Ettenbeuren (750–800 mm). Mean annual temperature is 7°–8°C at all sites. The forests surrounding the study sites are dominated by Norway spruce as a consequence of intensive forest management over centuries. Walentowski et al. (2006) includes this region in the collin and high montane beech forest zone.

Phytophagous species exhibit high seasonal and annual variation (e.g., Southwood et al. 2004; Goßner 2006, 2008).

Hence, to sample phytophagous communities, representative sampling should occur over the entire vegetation period of at least two consecutive years. We therefore aimed for long-term sampling at a restricted number of sites instead of nonrepresentative snapshots at many sites. For Douglas-fir, six stands of different tree species composition were investigated: two beech-dominated stands with interspersed Douglas-fir (DfBe1, DfBe2; both in Oberschönegger Forst), two Norway spruce-dominated stands with interspersed Douglas-fir (DfNs1, DfNs2; both in Oberschönegger Forst) and two Douglas-fir-dominated stands (DfDf1, DfDf2; both in a private forest near Edelstetten). The proportion of beech in the upper canopy ranged from 0% (DfDf1/DfDf2) to 10% (DfNs1), 23% (DfNs2), 64% (DfBe1), and 69% (DfBe2). For red oak, one mixed, broad-leafed stand with interspersed red oak (RoBe; in Ettenbeurer Forst) was studied. The number of plant species in the stands and coverage of different layers varied between stands. Douglas-fir-dominated stands showed the lowest cover of the canopy layer and the highest cover and species richness of the herb layer, while the canopy layer in the beech- and Norway spruce-dominated stands was denser, and consequently, the cover of the herb layer was low. Norway spruce-dominated stands also harbored a conspicuous dense moss layer. Details of the vegetation cover of the studied stands can be found in table A1 in the online edition of the *American Naturalist*.

Sampling Design

Insects were sampled during the vegetation period of three consecutive years (May–October 1999 and March–October 2000 and 2001). For studying phytophagous communities of particular tree species, flight-interception traps were installed in the center of the tree crowns (see Goßner 2004). This type of trap permits comprehensive sampling of the entire volatile fauna across multiple seasons (Basset et al. 1997). We did not consider using branch ectectors because they sample almost no additional phytophagous species (Coleoptera, Heteroptera). Even flightless species like *Strophosoma melanogrammum* (Coleoptera) are sampled representatively by flight-interception traps (Schubert 1998; Goßner 2004). In contrast, for studying phytophages in the vegetation near ground, flight-interception traps alone are not sufficient because in this environment they do not sample less flight-active species (mostly brachypterous Heteroptera, like Tingidae [*Acalypta musci*] and Miridae [*Bryocoris pteridis*]). These species are successfully trapped by pitfall traps (Barber 1931) and ground photo-ectectors (Engel 1999; M. M. Goßner, unpublished data). Hence, for near-ground vegetation studies, we used these trap types in addition to flight-interception traps, which we installed at a height of 1.5 m (table 1). Note, however, that

results based on all traps types or only flight-interception traps yielded similar results.

Studied Insect Taxa

Different sampling methods are recommended for representatively sampling different arboricolous insect taxa (Basset et al. 1997). While Lepidoptera might be comprehensively sampled by canopy fogging (caterpillars) or light trapping (adults), flight-interception traps are recommended for sampling Coleoptera and Heteroptera. We had to restrict ourselves to one sampling method, but we aimed to study phylogenetically and ecologically different insect taxa. Hence, two different taxa of phytophages of different levels of specialization and phylogenetic age were selected: the more ancient and more specialized, plant-sap-sucking Heteroptera and the younger, leaf-chewing Coleoptera.

Additionally, among Coleoptera, older clades that evolved before the angiosperm radiation in the early Cretaceous (Elateridae, Chrysomelidae, Byrrhidae, Carabidae, Neomychidae, Scarabaeidae, Staphylinidae) and younger clades that evolved and diversified at the time of the angiosperm radiation (Curculionidae, Apionidae, Kateritidae, Nitidulidae, Phalacridae, Rhynchitidae, Byturidae) were analyzed separately (for details, see table B1 in the online edition of the *American Naturalist*). Classification of phytophagous species of Coleoptera was done according to the methods of Köhler (1996, personal communication). In Heteroptera, all species for which plant sap is a major source of nutrients during their life span were included in the analysis. Classification was according to Péricart (1983, 1998), Wheeler (2001), and Wachmann et al. (2004). In neither taxon has any species specialized to the exotic tree species in its native range been introduced to central Europe (Kinzelbach et al. 2002). A list of all sampled species is published by Goßner (2004).

Data Analysis

For all analyses, data were pooled within stratum and tree species of each stand. We described faunal similarity between phytophages on each of the exotic tree species (Douglas-fir or red oak) and those on native tree species of the same versus different lineages. We considered two scales: (1) between gymnosperms and angiosperms, Douglas-fir was compared with Norway spruce and beech (data pooled from four replicate stands, years 1999–2001), and red oak was compared with pedunculate oak and Norway spruce (one stand, year 2000); (2) within gymnosperms or within angiosperms, Douglas-fir was compared with Norway spruce and the less closely related silver fir (following classifications of Liston [1996], Wang et al. [2000], and Eckert and Hall [2006]; one stand, years 2000–2001), and red oak

was compared with pedunculate oak and the less closely related beech (following classification of Manos et al. [2001]; one stand, years 2000–2001).

To test the role of mass effects, we first measured the similarity between phytophages of Douglas-fir and of the very distantly related beech, and then we asked whether similarity increased as beech became more abundant. Specifically, we compared the faunal similarity between Douglas-fir and beech with that between Douglas-fir and the closely related Norway spruce, replicated across four stands of increasing proportion of beeches in the canopy. Second, we compared the faunal similarity between either of the two exotic tree species and its respective most closely related native tree species (Douglas-fir/Norway spruce, red oak/pedunculate oak) with the similarity between the exotic tree and the vegetation near the ground (which is at least intermediately distantly related). Note that vegetation near the ground today largely reflects that which existed when the trees were planted, as these stands have a long tradition of wood production. The generally high abundance of near-ground vegetation during tree establishment could have caused mass effects, that is, the vegetation near the ground being the major source of colonizers. Since then, the faunal composition may have been conserved within trees and, still in today's mature trees, fauna may more closely resemble that in the vegetation near the ground than that in (phylogenetically more closely related) ambient tree species. For Douglas-fir, data from six stands were pooled because trend patterns over stands were consistent.

We used two types of dissimilarity indexes to compare faunas: (1) the Morisita dissimilarity index (Morisita 1959), which is defined as 1 minus the Morisita similarity index and is based on the Simpson concentration (Simpson 1949; Jost 2006), and (2) the jackknifed-Horn dissimilarity index, which is a jackknifed version of a heterogeneity measure (Horn 1966) based on Shannon's entropy.

The Morisita (1959) index is disproportionately influenced by common species; relatively rare species have little effect. Its estimator (Krebs 1999, p. 391) is dominated by abundant species and is likely to be resistant to undersampling because the influential abundant species are always present in samples (Chao et al. 2005, 2006). Note that abundant species are not necessarily more generalist; in fact, for Heteroptera on oaks, the inverse is true (Goßner 2008). Horn's index weights all species by their frequencies, without favoring either common or rare species (Jost 2006, 2007). However, moderate undersampling bias may exist in Horn's estimate. We applied the jackknife method proposed by Schechtman and Wang (2004) to remove most of the undersampling bias. The jackknife method originally developed by Quenouille (1949) for single-sample data is a useful technique for reducing bias of an estimate (see Mil-

Table 1: Sampling design of the Douglas-fir and the red oak approaches

Component	Douglas-fir					Red oak	
	DfDf1	DfDf2 ^a	DfNs1	DfNs2	DfBe1	DfBe2	RoBe
Studied tree species	Df, Ns	Df, Ns	Be, Df, Ns, Sf ^b	Be, Df, Ns	Be, Df, Ns	Be, Df, Ns	Be, Ns ^c , Po, Ro
Comparisons	Df/Ns vs. Df-NG	Df/Ns vs. Df-NG	DF/Ns vs. Df/Be; Df/Ns vs. Df/Sf; Df/Ns vs. Df-NG	DF/Ns vs. Df/Be; Df/Ns vs. Df-NG	DF/Ns vs. Df/Be; Df/Ns vs. Df-NG	DF/Ns vs. Df/Be; Df/Ns vs. Df-NG	Ro/Po vs. Ro/Ns; Ro/Po vs. Ro/Be; Ro/Po vs. Ro/NG
Sampling period:							
Canopy	1999–2001	1999–2001	1999–2001	1999–2001	1999–2001	1999–2001	2000–2001
Near ground	1999–2000	1999–2000	1999–2000	1999–2000	1999–2000	1999–2000	1999–2000
Canopy traps:							
Flight interception	6	6	12	9	9	9	21
Near-ground traps:							
Pitfall	8	8	8	8	8	8	8
Ground photoeclector	3	3	3	3	3	3	3
Flight interception	3	3	3	3	3	3	3

Note: Studied tree species, the comparisons of faunal dissimilarity for which the stands were used, sampling period, and number of traps are given for each studied stand (independent replicate). Studied tree species: beech (*Fagus sylvatica*; Be); Douglas-fir (*Pseudotsuga menziesii*; Df); Norway spruce (*Picea abies*; Ns); pedunculate oak (*Quercus robur*; Po), red oak (*Quercus rubra*; Ro), silver fir (*Abies alba*; Sf).

^a Because Hurricane Lothar destroyed this stand in winter 1999–2000, traps were installed in a nearby stand in 2000.

^b Silver fir was sampled in the years 2000 and 2001, and in one stand only. For the comparison of canopy communities between Douglas-fir, Norway spruce, and silver fir (within-gymnosperm approach), only data from 2 years and one stand were analyzed.

^c Norway spruce, planted at the border of the adjacent deciduous forest stand RoBe, was sampled only in the year 2000. For the comparison of canopy communities between red oak, pedunculate oak, and Norway spruce (between angiosperm and gymnosperm approach), only data from 1 year were analyzed.

ler 1974 for a review). This method has been extended by Schechtman and Wang (2004) to deal with multiple-sample data.

Our quantifications of the faunal dissimilarity are thus based on abundance data. We consider quantifications using abundance data to be ecologically more meaningful than those using incidence data, that is, presence or absence of species. A maple forest with one pine tree is not ecologically identical to a pine forest with one maple tree, but incidence-based similarity measures would find them identical. Thus, we do not consider the use of the traditional incidence-based Jaccard or Sørensen indices. In our particular case, the rare species—which would have the same weighting as abundant species using incidence-based indices—may sometimes be a tourist species caught by the traps while passing by. Incidence-based measures are subject to further bias that is statistically difficult to adjust when there are unseen species (see Chao et al. 2006). Furthermore, abundances of phytophages are important for plant-animal interactions. Finally, the fact that our flight-interception traps sample “activity abundances” instead of “true abundances” would only bias results if activity of species would systematically change as a function of the phylogenetic position of their host species, which is unlikely.

Our analysis is mainly based on statistical inference for the difference between two dissimilarity indices. For example, when we assess whether and to what extent faunas on an exotic tree species are more similar to faunas on closely related species than to those on distantly related native trees, we define a measure of the effect size of the difference between faunas on exotics and faunas on natives: $Q = \text{dissimilarity index (exotic/more closely related native)} - \text{dissimilarity index (exotic/more closely related native)}$. From a statistical point of view, we must provide information regarding how big and ecologically important the difference is. Using abundance data, we provide an estimate for Q to quantify the extent of the effect. We also obtain a standard error (SE) for the estimate and use it to construct a 95% confidence interval for the difference. Methods are briefly described in the next paragraph. A confidence interval provides a plausible range for the magnitude of the effect size. If the confidence interval covers a range of large values, we can conclude that the effect is high. On the other hand, if it covers only small values, then we can conclude that the effect is low.

Because of the close link between a confidence interval and hypothesis testing (e.g., Gardner and Altman 1986; Schenker and Gentleman 2001), a confidence interval of difference can also indicate whether the two dissimilarity indices are significantly different. That is, if the confidence interval does not cover 0, then we conclude that the two indices are significantly different. Otherwise, it implies that

0 is a plausible value for the difference and thus that the difference is not significant.

In our model, we assumed that, for each community, the sample frequencies follow a multinomial distribution with cell probabilities being equal to species' relative abundances (namely, data are representative of the true community). An SE estimate was calculated from 500 bootstrap replications from such an assumed model. A 95% confidence interval of the difference is calculated this way: lower bound = estimate $- 1.96$ SE, upper bound = estimate $+ 1.96$ SE. Generally, the length of a confidence interval reflects the amount of information in the data. Sparse data typically yield a relatively wide interval.

Results

Regarding Douglas-fir comparisons, we found 6,025 Coleoptera of 71 species and 2,099 Heteroptera of 47 species; regarding red oak comparisons, we found 1,957 Coleoptera of 67 species and 771 Heteroptera of 37 species. We found Heteroptera from five families and Coleoptera from 14 families; of the latter, seven were ranked as old and seven were young (see “Material and Methods”). Details can be found in tables C1 and C2 in the online edition of the *American Naturalist*.

Similarity of Communities in the Canopy of Exotic and More or Less Closely Related Native Trees

Between Angiosperms and Gymnosperms

Coleoptera and Heteroptera communities on exotic Douglas-fir were significantly more similar to those on closely related native Norway spruce (dissimilarity values were < 0.1 ; see table D1 in the online edition of the *American Naturalist*) than to those on distantly related native beech. Using jackknifed-Horn dissimilarity indices (characterizing the entire community, including rare species; fig. 1a), the confidence interval for Q did not overlap with 0, indicating significance. The difference was much greater in Heteroptera (dissimilarity values: Douglas-fir/Norway spruce = 0.05, Douglas-fir/beech = 0.55) than in Coleoptera (Douglas-fir/Norway spruce = 0.03, Douglas-fir/beech = 0.07; table D1). This was confirmed by analysis based on Morisita indices (emphasizing numerically dominant species) for Heteroptera (Douglas-fir/Norway spruce = 0.02, Douglas-fir/beech = 0.78) but not for Coleoptera (Douglas-fir/Norway spruce = 0.05, Douglas-fir/beech = 0.04), where the difference proved to be nonsignificant.

Similar results were obtained for red oak (fig. 1b). Here, the confidence intervals are wider because of less data. Communities of Coleoptera and Heteroptera on this exotic tree species were clearly more similar to those on the na-

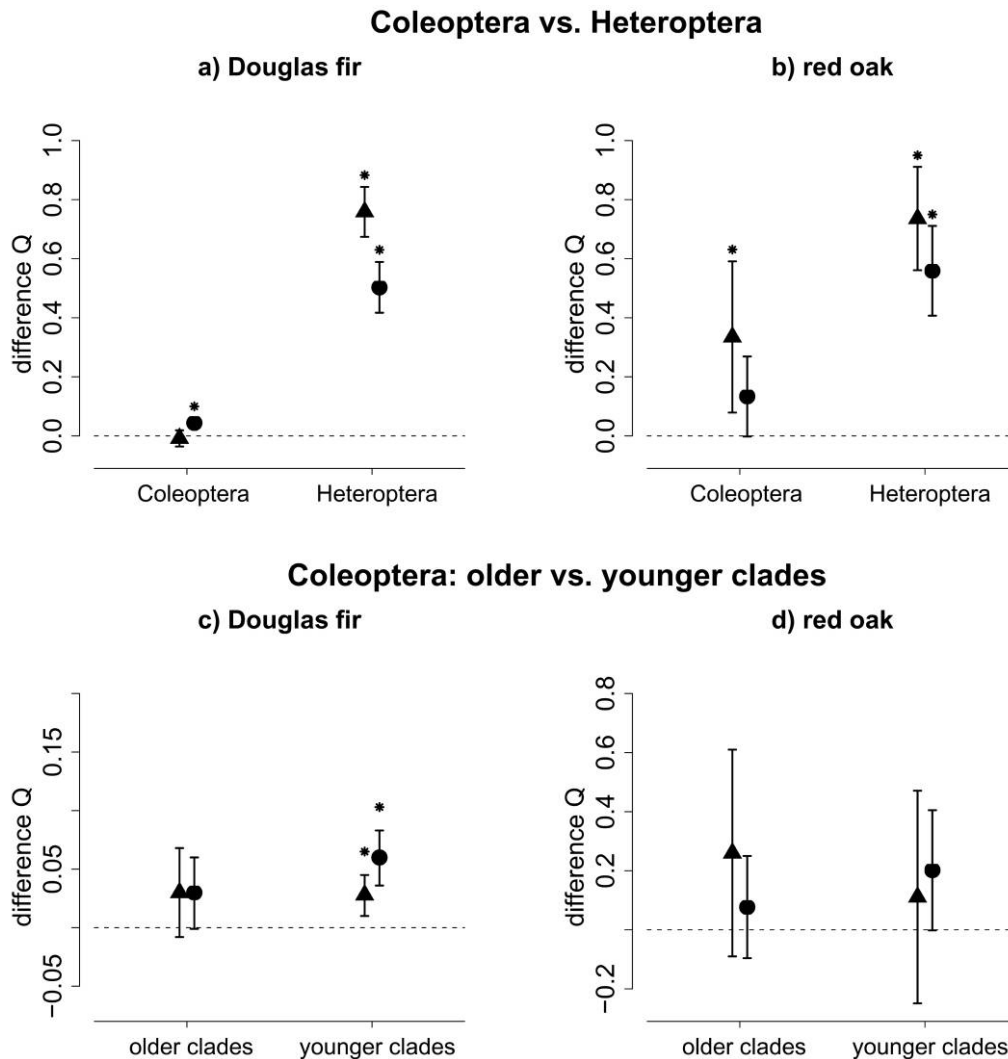


Figure 1: Dissimilarity of faunas on exotic tree species compared with those on closely related native tree species (from the same family) and on very distantly related native tree species (from a different phylum). Dissimilarity is quantified for dominant species (Morisita index; *triangles*) and for all species (jackknifed-Horn index; *circles*), respectively, and is given as the difference Q between (exotic/very distantly related native) and (exotic/closely related native), including its 95% confidence limit. An asterisk indicates that the confidence interval excludes 0, and as such the fauna on the exotic tree species is significantly more different from that on the very distantly related tree species than it is from that on the closely related native species. Averages of Morisita and jackknifed-Horn indices for Coleoptera and Heteroptera are given in table D1 in the online edition of the *American Naturalist*. Data were pooled across four forest stands for Douglas-fir and one forest stand for red oak, with three trees per stand and species. For the red oak, comparison data are restricted to 1 year because Norway spruce was sampled in 2000 only (see table 1). All comparisons for a given alien tree species are based on the same stand(s). Overall, heteropteran faunas on the exotic species resemble those on the closely related native species more than those on the very distantly related native species, whereas for coleopterans, this effect is weaker and depends on tree species, family age, and dissimilarity measure.

tive, closely related pedunculate oak than on the native, very distantly related Norway spruce. Effects of relatedness between trees were less conspicuous than they were in Douglas-fir, but again effects were stronger for Heteroptera (mean dissimilarity values: red oak/pedunculate oak = 0.21–0.22, red oak/Norway spruce = 0.78–0.95) than for Coleoptera (red oak/pedunculate oak = 0.03–0.16, red

oak/Norway spruce = 0.29–0.36; table D1). In Coleoptera, significant differences were observed only for dominant species (Morisita index; fig. 1b).

By analyzing older and younger clades among Coleoptera separately, we found that, for younger clades, Douglas-fir recruited significantly more from closely related Norway spruce than from distantly related beech (Morisita and

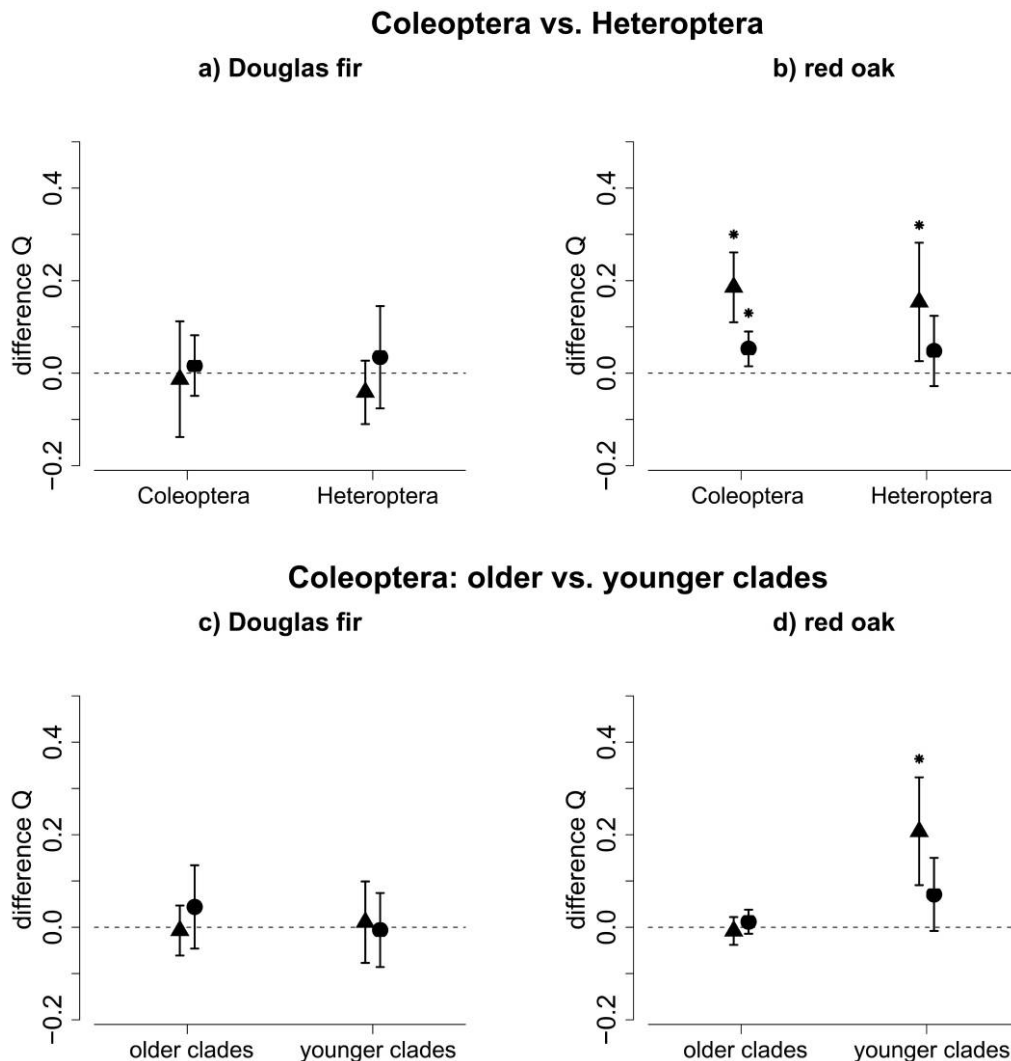


Figure 2: Dissimilarity of faunas on exotic tree species compared with closely related native tree species (from the same family) and moderately distantly related native tree species (from a different family of the same phylum). Dissimilarity is quantified for dominant species (Morisita index; triangles) and for all species (jackknifed-Horn index; circles), respectively, and is given as the difference Q between (exotic/very distantly related native) and (exotic/closely related native), including its 95% confidence limit. An asterisk indicates the confidence interval excludes 0, and as such the fauna on the exotic tree species is significantly more different from that on the moderately distantly related tree species than it is from that on the closely related native species. Averages of Morisita and jackknifed-Horn indices for Coleoptera and Heteroptera are given in table D1 in the online edition of the *American Naturalist*. Data are based on one stand and 2 years in all comparisons. Note that different data subsets used in figures 1 and 2 resulted in different values. A total of three trees per tree species for Douglas-fir comparisons and six trees per tree species for red oak comparisons were sampled (see table 1). All comparisons for a given alien tree species are based on the same stand(s). Faunas on the exotic species resemble those on the closely related native species more than those on the moderately distantly related native species, mainly in young Coleoptera clades on angiosperms.

jackknifed-Horn index; fig. 1c); this effect of relatedness was nonsignificant for older clades. However, effect size was relatively low, even for younger clades (confidence intervals cover only small values; fig. 1c). Regarding red oak, we found no difference between younger and older clades and no significant effects (fig. 1d).

Within Angiosperms or within Gymnosperms

Within gymnosperms, communities (of both Heteroptera and Coleoptera) on Douglas-fir did not resemble those on the closely related Norway spruce more than those on the more distantly related silver fir (fig. 2a). Generally, dissim-

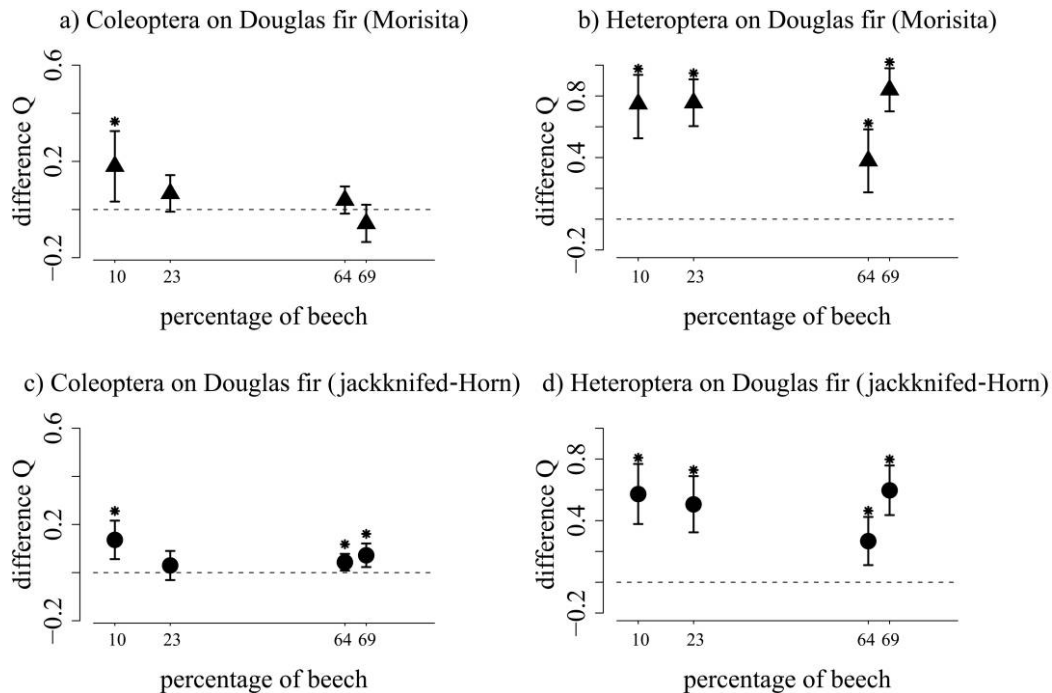


Figure 3: Dissimilarity of faunas on exotic tree species compared with those on closely related native tree species (from the same family) and on very distantly related native tree species (from a different phylum) in forest stands of increasing density of the very distantly related tree species. Dissimilarity is quantified for dominant species (Morisita index; triangles) and for all species (jackknifed-Horn index; circles), respectively, and is given as the difference Q between (exotic/very distantly related native) and (exotic/closely related native), including its 95% confidence limit. An asterisk indicates the confidence interval excludes 0, and as such the fauna on the exotic tree species is significantly more different from that on the very distantly related tree species than it is from that on the closely related native species. Data are based on a total of three trees per tree species and stand. Note that coleopteran faunas on Douglas-fir match those on the very distantly related beech where it dominates the canopy, whereas heteropteran faunas remain distinct even then.

ilarities between communities were low, reaching values of 0.1 or less (see table D1).

Within angiosperms, faunal similarities between the exotic red oak and the closely related pedunculate oak were significantly larger than faunal similarities between red oak and the more distantly related beech (fig. 2b), the only exception being the dominant species of Heteroptera as quantified by the Morisita index. However, the effect sizes were relatively low (confidence intervals cover a range of small values), and so were the dissimilarities between communities in Coleoptera (mean dissimilarity values: red oak/pedunculate oak: 0.03–0.08; red oak/beech: 0.13–0.22) and Heteroptera (red oak/pedunculate oak: 0.11–0.13; red oak/beech: 0.16–0.28; table D1).

Neither in older nor in younger clades of Coleoptera did Douglas-fir recruit more phytophages from closely related compared with moderately distantly related tree species. However, in angiosperms, similarity of phytophage communities of younger clades between red oak and closely related pedunculate oak was greater than between red oak and moderately distantly related beech. With re-

spect to dominant species (Morisita index), the difference was significant; with respect to all species, it was close to significant. In older clades, no differences were observed.

Mass Effects

Communities on Douglas-Fir Depending on Proportion of Beech in the Canopy

Heteroptera communities on Douglas-fir were significantly more different from those on the very distantly related beech than those on the more closely related Norway spruce, even if beeches were highly dominant in the surrounding canopy (fig. 3). However, Coleoptera communities on Douglas-fir resembled those on Norway spruce more strongly than those on beech only where beech was rare (<10%; fig. 3). With an increasing proportion of beech in the canopy, the fauna on Douglas-fir increasingly resembled that on beech. In beech-dominated canopies, Douglas-fir even recruited more of its dominant Cole-

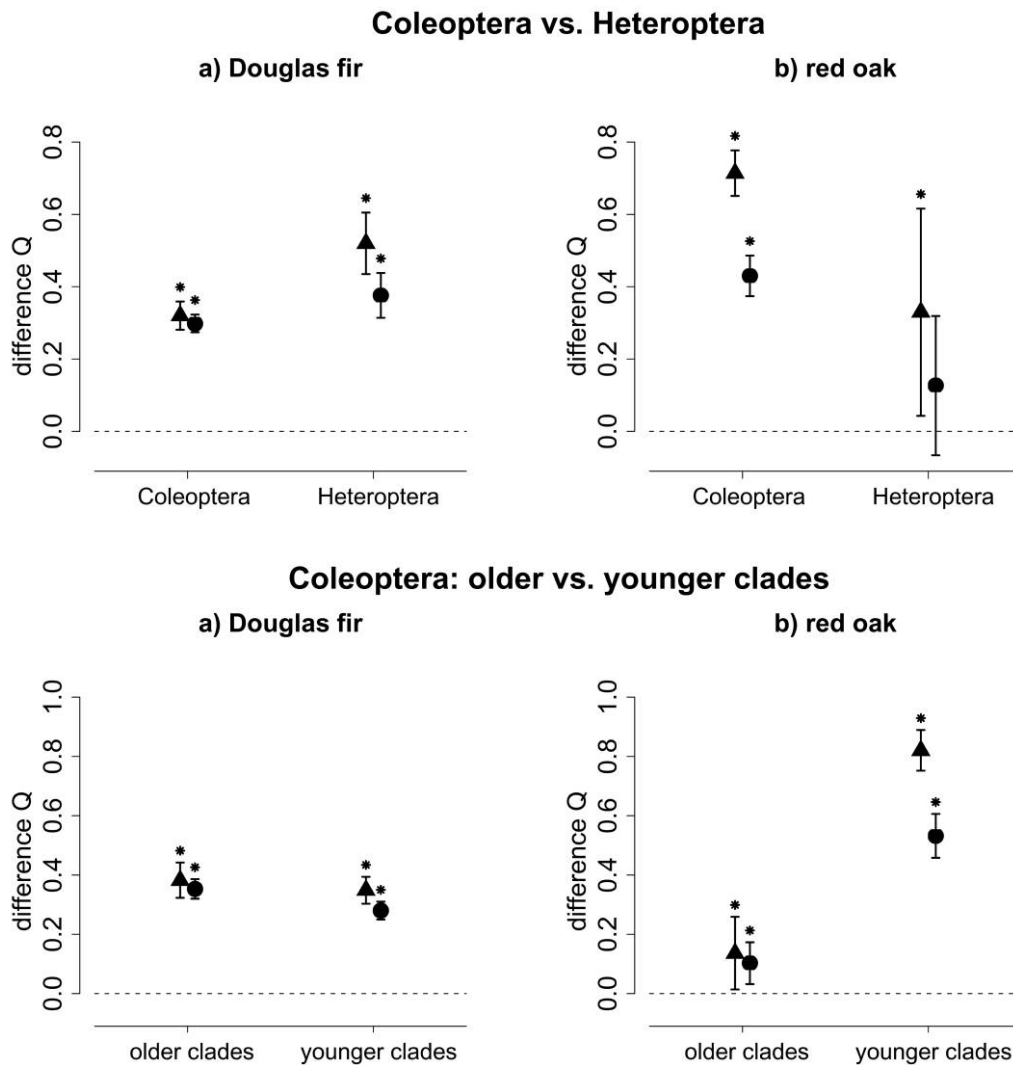


Figure 4: Dissimilarity of faunas on exotic tree species compared with closely related native tree species (from the same family) and to the more distantly related vegetation near the ground. Dissimilarity is quantified for dominant species (Morisita index; *triangles*) and for all species (jackknifed-Horn index; *circles*), respectively, and is given as the difference Q between (exotic/very distantly related native) and (exotic/closely related native), including its 95% confidence limit. An asterisk indicates the confidence interval excludes 0, and as such the fauna on the exotic tree species is significantly more different from that on the moderately distantly related tree species than it is from that on the closely related native species. Averages of Morisita and jackknifed-Horn indices for Coleoptera and Heteroptera are given in table D1 in the online edition of the *American Naturalist*. Note that differing data subsets used in figures 1, 2, and 4 resulted in different values (see table 1). Data were pooled across six forest stands for Douglas-fir; see figure 1 for further details. Overall, faunas on the exotic species resemble those on the closely related native species more than those in the distantly related vegetation near the ground, especially in younger clades of Coleoptera. Note that Heteroptera data were quite sparse for the ground stratum.

optera species from beech than from Norway spruce (fig. 3, Morisita index).

While no mass effect was observed in older clades of Coleoptera, we found that, for younger clades, dissimilarity between Douglas-fir and beech decreased significantly with increasing proportion of beech in the surroundings (not shown).

Similarity of Communities in the Canopy of Exotics and in the Vegetation Near the Ground

In both Coleoptera and Heteroptera and for both dissimilarity indices, communities in Douglas-fir were significantly and considerably more similar to those on related Norway spruce (dissimilarity values were <0.2 in Heteroptera and

<0.05 in Coleoptera; see table D1) than to those near the ground (fig. 4a). The difference was greater in Heteroptera than in Coleoptera. Moreover, communities on Douglas-fir and those near the ground were much more dissimilar in Heteroptera (dissimilarity values: Douglas-fir/Norway spruce = 0.15–0.20, Douglas-fir/near ground = 0.52–0.72) than in Coleoptera (Douglas-fir/Norway spruce = 0.02–0.04, Douglas-fir/near ground = 0.30–0.32; table D1).

Similar results were observed regarding communities on red oak, which were more similar to those of congeneric pedunculate oak than to those near the ground (fig. 4b). The only exceptions were Heteroptera as quantified by the jackknifed-Horn index (i.e., including rare species), but this may be due to the limited sample size at ground level (27 specimens, 14 species), which resulted in wide confidence intervals. Overall, differences were greater in Coleoptera than in Heteroptera (confidence intervals cover a range of higher values in Coleoptera; fig. 4b). Moreover, dissimilarities between communities on red oak and those near the ground in Coleoptera (mean dissimilarity values: red oak/pedunculate oak = 0.03–0.08, red oak/near ground = 0.51–0.75) were almost twice as high as those in Heteroptera (red oak/pedunculate oak = 0.11–0.13, red oak/near ground = 0.24–0.46; table D1).

The general trend that was observed in regard to all Coleoptera could also be confirmed for a separate analysis of older and younger Coleoptera clades. Interestingly, on red oak, the effects were much stronger for younger than for older clades (higher effect size indicated by a range of high values covered by confidence intervals in fig. 4).

Discussion

Phylogenetic Conservatism versus Geographic Contingency

In this study, we tested for the first time to what extent phylogenetic conservatism in the assembly of local phytophage communities is reduced when host plants and phytophages become separated for millions of years on different continents. We found that overall faunal similarity between exotic and native trees was weaker between than within plant phyla, indicating strong phylogenetic conservatism. It is known that chemical and physical traits are more similar within than between plant phyla, which facilitates host shifts between closely related plant species in insect herbivores (Conner et al. 1980; Strong et al. 1984; Becerra 1997). However, most previous studies were based on compilations of species lists, and they found only a weak correlation between taxonomic relatedness and species richness of phytophages on trees (e.g., Kennedy and Southwood 1984; Brändle and Brandl 2001). Faunal similarity was not analyzed in these studies. Our results, based on a local community approach, demonstrate that the im-

portance of phylogenetic proximity in the colonization process of trees might be stronger than assumed by these studies of species richness. Only Brändle and Brandl (2006) found a strong negative correlation between similarities of phytophage assemblages and genetic distances among native host genera, with again by far the greatest differences between gymnosperm and angiosperm genera. This coincides with the major differences between these plant phyla in morphology (Sitte et al. 2002), biomass partitioning (Enquist 2003), and secondary plant compounds (Strong et al. 1984). Our study reveals that the assembly of phytophage communities on angiosperms versus those on gymnosperms is phylogenetically conserved not only among trees that have coevolved with their faunas in the same geographic region but also among tree species that have been separated for millions of years on different continents and are then brought back in contact.

The two phytophage taxa we studied showed different scales of phylogenetic conservatism. While sap-feeding Heteroptera were highly dissimilar between very distantly related tree species, chewing Coleoptera were only moderately dissimilar on this scale. One might hypothesize that this difference relies on the different feeding modes in Heteroptera and Coleoptera. Two hypotheses potentially explain differences in dissimilarity of phytophagous communities between sap feeders and chewers, resulting in opposite predictions with respect to our system. (1) Sap feeders feed on internal leaf tissue and fluids and therefore might circumvent physical barriers better than external feeders (Tallamy 1986; Cornell 1989; Cornell and Kahn 1989). According to this hypothesis, sap feeders may be expected to cope better with the very different physical barriers in gymnosperms and angiosperms than external feeders. (2) Sap feeders, like other externally living but internally feeding species, are considered to be more specialized than external feeders (Frenzel and Brandl 2003). In a study focused on specialization in different insect taxa, Mattson et al. (1988) confirmed this for sap feeders compared with chewers. Accordingly, sap-feeding Heteroptera may be expected to cope less well with differences between gymnosperms and angiosperms than Coleoptera. Indeed, we found that sap feeders are less similar between gymnosperms and angiosperms than chewers. Thus, we hypothesize that the level of specialization required for internal feeding may be relatively more important than that required for overcoming external physical differences. Consequently, sap-feeding Heteroptera may need longer to colonize a new host species (Strong et al. 1984), in particular, a distantly related one, resulting in high faunal dissimilarity (see also Brändle and Brandl 2001, 2006). Testing these hypotheses of the effect of feeding type on phylogenetic host conservatism will require data on further sap-feeding (such as Homoptera: Aphidina, Cicadina,

Psyllidae; Thysanoptera) and chewing (such as Lepidoptera; Hymenoptera: Symphyta; Orthoptera) insect taxa.

Between moderately distantly related tree species within the same phylum, phylogenetic conservatism in the recruitment of phytophages was observed only on the angiosperm red oak, not on the gymnosperm Douglas-fir. While general conclusions regarding differences between angiosperms versus gymnosperms cannot be made on the basis of a single comparison, we suggest a hypothesis for why phylogenetic conservatism in the recruitment of phytophages may be stronger among angiosperms. Diversity of allelochemical compounds is greater among angiosperms than among gymnosperms. For example, in contrast to woody gymnosperms, woody angiosperms contain hydrolyzed tannins as well as condensed tannins (Harborne 1995). This might potentially lead to greater host specificity and fewer opportunities for host shifts among Fagaceae than among Pinaceae. Thus, we suppose that adaptations needed for a host shift from a native to an exotic Pinaceae are less important than those needed to shift between different Fagaceae hosts. Future tests of this hypothesis will require data on further angiosperm and gymnosperm aliens, belonging to further families.

On angiosperm trees, only the coleopteran fauna was significantly more dissimilar between the exotic and the moderately distantly related compared with closely related native tree species. This might be linked to differences in phylogenetic age of Coleoptera and Heteroptera and of angiosperm and gymnosperm trees. Several studies demonstrated that ancient plant lineages are colonized by a high proportion of phytophages from ancient lineages (Zwölfer 1978; Ward et al. 2003). Moreover, as exemplified by beetles, Farrell (1998) demonstrated a pronounced conservatism in the evolution of insect-plant associations. According to Strong et al. (1984), phytophagy evolved earlier in Heteroptera (~185 million years ago) than in Coleoptera (~135 million years ago). Therefore, Heteroptera are the more ancient of the two phytophage taxa, and gymnosperms the more basal of the two tree taxa. Moreover, phytophagy in Heteroptera is older than the radiation of angiosperms in the Early Cretaceous (~130 million years ago). Consequently, Heteroptera may be evolutionarily more strongly linked to gymnosperms, and beetles may be evolutionarily more strongly linked to angiosperms, with coleopteran communities strongly matching the phylogenetic proximity of their angiosperm hosts.

More support for this hypothesis arises when older and younger clades among Coleoptera are analyzed separately. Communities of younger clades were more distinct between exotic red oak and native beech than between red oak and its closer relative pedunculate oak. Furthermore, assembly of younger Coleoptera clades on the exotic gymnosperms showed a significant signal of phylogenetic con-

servatism across phyla but not within. In contrast, on the exotic angiosperms, assembly of younger clades showed a significant signal of phylogenetic conservatism within a phylum but not across phyla. Older Coleoptera clades, sampled from the same trees, never showed phylogenetic signals. Younger clades diversified at the time of angiosperm radiation, and therefore they might be more strongly linked to angiosperms, whereas older clades are more closely linked to gymnosperms. To our knowledge, this is the first time that differences in the age of evolutionary diversification of major lineages have been shown to be related to differences in today's assembly of local communities.

Alternatively to this explanation based on historical sorting of Heteroptera and Coleoptera on angiosperms and gymnosperms, present-day interactions may be crucial. Heteroptera might displace Coleoptera from gymnosperms, rendering the distributions of Coleoptera on exotic Douglas-fir more stochastic and the inverse for Heteroptera on exotic oaks. However, we found no negative correlations of abundances between Coleoptera and Heteroptera (results not shown; see also Southwood et al. 2004).

Overall, for the majority of comparisons at the intermediate phylogenetic scale (within a phylum), we found no phylogenetic conservatism in the assembly of local phytophage communities on exotic tree species. For native oaks and beeches, however, Summerville et al. (2003) demonstrated the importance of phylogenetic proximity for the assemblages of phytophages. This indicates a strong element of geographic contingency: throughout the separation of millions of years and different continents, trees have evolved different traits, and regional phytophage faunas have adapted to these traits. When brought back into local contact, trees of the same lineage are no longer colonized by the same phytophage species; exotic trees may well recruit their phytophages from intermediately distantly related native trees from another family. Ricklefs and Latham (1992) found that plant species from the same genus occupied similar climatic niches in North America and East Asia; that is, geographic contingency was low. However, climate niches of plants may be evolutionarily more stable than their phytophage faunas. Contrary to climate, phytophages can actively choose or avoid plants and thereby induce dynamic disruptive selection pressures. This may increase the likelihood of shifts in the relationship between plants and phytophages. Emigration and reimmigration of plant hosts may thus often break up the control of phylogenetic conservatism on the assembly of local phytophage communities.

The Role of Local Mass Effect

In this study, we also tested for the first time whether phylogenetic conservatism in the assembly of local phytophage communities on an exotic host can be overridden by mass effects, that is, by the sheer size of the source pool on distantly related but highly abundant or spatially proximate hosts. Such mass effects may be particularly likely in polyphagous species, which can easily switch between host taxa; in fact, all species sampled from beech (except for two coleopterans) are polyphagous (Böhme 2001; Goßner 2008). We found that mass effects within the canopy could indeed partly override phylogenetic conservatism in the assembly of arthropod communities on exotics. Coleoptera faunas (in particular, younger clades) on Douglas-fir resembled those on the very distantly related beech where beeches dominated the canopy. For Heteroptera and older Coleoptera clades, in contrast, no such mass effects were observed. As already mentioned, Heteroptera and older clades of Coleoptera might be evolutionarily more strongly linked to gymnosperms. Therefore, phylogenetic conservatism may be more important in these taxa, while stochastic mass effects might play a more important role in the colonization process of exotic Douglas-fir by younger clades of phytophagous Coleoptera.

Faunas on exotic trees were always very distinct from those in the very distantly related near-ground vegetation. This may be because fauna from the herb and shrub layer that establish themselves in young crowns are replaced by canopy-dwelling species in old trees. Alternatively, even the young crowns may not be colonized from the adjacent herb/shrub layer because of very different habitat qualities in terms of secondary plant compounds, leaf phenology, and leaf and plant architecture (Niemelä and Haukioja 1982; Niemelä et al. 1982; Lawton 1983; Neuvonen and Niemelä 1983; Kennedy and Southwood 1984). Comparing these hypotheses is beyond the scope of this article.

Implications for the Role of Evolution in Community Assembly

Exploring the interface between community assembly and the evolution of lineages has been recognized as a major way to advance both fields (e.g., Webb et al.'s [2002] review article has been cited 199 times; Vamori et al. 2009). Surprisingly, the insights from this exercise seem to be quite contradictory and are rarely put into perspective, let alone reconciled. Some authors suggest that evolution acts sufficiently rapidly, and spatially it is fine-grained enough, to have a major effect on the assembly of local communities, resulting in geographical mosaics of coevolution between generalist species and rapid diversification in response to local and regional opportunities (Thompson 1999, cited

160 times). Other authors, in completely the reverse direction, argue that ecological sorting in the assembly of local communities leads to stabilizing selection, specialization, and ultimately evolutionary conservatism of traits and niches across millions of years (Ackerly 2003, cited 67 times). This study shows that phylogenetic conservatism can indeed be strong even after lineages are separated for millions of years, favoring the second of the two perspectives. However, across intermediate phylogenetic distances, phylogenetic conservatism in the phytophage fauna can indeed be overlaid in various situations by regional and local contingencies. In these cases, the evolutionary scenario may drastically change from stabilizing selection due to predictable, specialized interactions between particular plant species and particular phytophage species, to more variable, less predictable selection pressures with geographic diversification and increasingly convergent evolution of plant/phytophage associations (Thompson 1999). Moreover, populations may become increasingly regulated by idiosyncratic interactions between pairs of species that happen to come into contact locally (Price 2003). This partial disappearance of phylogenetic conservatism in phytophage community assembly at intermediate phylogenetic scales may have resulted from the separate evolution of tree lineages on different continents, followed by intercontinental dispersal. Intercontinental dispersal may thus strongly contribute to the breaking up of long-evolved plant-insect relationships (Labandeira 2002). Intercontinental dispersal has occurred throughout the history of life, but today it is strongly influenced by humans.

Conclusion

In this study, we tested the role of phylogenetic conservatism versus geographic contingency and local mass effects in the assembly of local phytophage communities. We studied two cases: two alien tree species, colonized by two major phytophage taxa originating from more or less closely related native host plants. Although it was a major effort (>10,000 individuals were sampled and determined), a study on two cases does not allow final conclusions on assembly of phytophage communities in general; rather, it should be taken as a first step into a new research area. On the basis of the results of this study, we suggest that similarity in chemical and physical traits of phylogenetically related tree species might be the most important factor in the colonization process of exotic as well as native tree species. Ecological factors such as co-occurrence of tree species in the same habitat (mass effects) or regionally different traits and constraints of herbivore taxa (geographical contingency) might also contribute to this process, but they may be of minor importance at large phy-

logenetic scales. Overall, phylogenetic conservatism can drive the assembly of phytophage faunas even on exotic trees, despite millions of years of separate evolution. Whether it outweighs geographic contingency and mass effects may depend on the phylogenetic scale, local abundance of native tree species, and phytophage taxon, with taxa being more conservative on tree lineages with which they codiversified. This complex interplay will determine the degree to which present-day plant-insect interactions are constrained by tens of millions of years of evolutionary history.

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Installation of flight-interception traps on exotic Douglas-fir about 35 m within a conifer stand (*left*) and a beech stand with interspersed Douglas-firs in southern Germany (*right*). Photographs by K. Deiters.